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Do non-estuarine mangroves harbour higher densities of juvenile fish than adjacent shallow-water and coral reef habitats in Curaçao (Netherlands Antilles)?

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ABSTRACT: Most mangroves occur in tropical estuaries and generally contain higher densities of fish than adjacent habitats such as seagrass beds and sand flats. The question of whether these fishes depend on estuaries per se has given rise to the concept of estuarine-dependence. On several Caribbean islands, mangroves are only found in non-estuarine bays and lagoons. To test whether fishes also depend on mangroves in non-estuarine conditions we determined juvenile and adult densities of a complete reef fish community in 4 bay habitats (mangrove, seagrass bed, channel, subtitdal mud flat) in the Spanish Water Bay and 4 depth zones (2, 5, 10 and 15 m depth) on the adjacent coral reef of the Caribbean island of Curaçao (Netherlands Antilles), using a single visual census technique in all habitats. The results showed that non-estuarine mangroves did harbour a much higher total juvenile fish density, density of juvenile temporary bay residents (i.e. nursery species), and density of juvenile permanent bay residents (i.e. bay species) than adjacent seagrass beds, channel and mud flats, but a similar total juvenile fish density as the coral reef. The different patterns of abundance of juvenile fish are probably related to the degree of structural habitat complexity. For a number of nursery and bay species, juvenile fish were found almost exclusively in the mangroves and sometimes to a lesser extent in other bay habitats, but rarely on the coral reef, giving rise to the concept of 'bay habitat dependence'. Juvenile and adult habitats differed for at least 21 of the 50 most common reef species, suggesting partial or complete ontogenetic habitat shifts from the mangroves to the reef, from the channel to the reef, and from the shallow to the deeper coral reef. Different associations with habitat type were also found at the level of fish families.

KEY WORDS: Coral reef fish · Mangroves · Seagrass beds · Coral reef depth zones · Habitat utilisation · Ontogenetic shifts

INTRODUCTION

Fish population size and structure in shallow coastal habitats such as coral reefs show large temporal and spatial variation (Williams 1991). Several presettlement and postsettlement factors are responsible for this. Presettlement factors include duration of plankton larval stage and degree of larval input, whereas postsettlement factors include degree of recruitment, early postsettlement migration, intraspecific competition, postsettlement predation and mortality, and habitat complexity (Doherty 1991, Jones 1991, Leis 1991). In the postsettlement phase, habitat utilisation is often associated with foraging demands, predator avoidance or reproduction (Sutherland 1996), and is generally a trade-off between growth rate and predation risk (Werner et al. 1983, Lima & Dill 1990).

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Since food requirements and predation risk change during ontogeny, shifts in habitat occur to meet the changing demands of fishes (Ludwig & Rowe 1990). One of the underlying ecological processes of ontogenetic habitat shifts has been suggested to be the 'minimise μ/g hypothesis', which states that habitats are selected where growth rate (g) is maximised and mortality risk (μ) is minimised (Utne et al. 1993, Dahlgren & Eggleston 2000). The strong selection for maximising growth rates has several advantages, such as reducing the amount of time to reach maturity, and an increase in size resulting in higher fecundity and higher survivorship (Werner & Gilliam 1984).

Various reef-associated fish species utilise off-reef habitats such as mangroves and seagrass beds located in estuaries, lagoons or bays as nurseries during their juvenile life stage (Parrish 1989). The selection of such habitats is probably based on the 'minimise μ/g hypothesis' and several related hypotheses have been proposed to explain the high densities of juvenile fishes in these habitats: (1) these habitats provide a great abundance of food for fishes (Carr & Adams 1973, Ogden & Zieman 1977); (2) the structural complexity of these biotopes provide excellent shelter against predators (Parrish 1989, Robertson & Blaber 1992); (3) these biotopes are often located at a distance from the coral reef or from offshore waters and are therefore less frequented by predators (Shulman 1985, Parrish 1989); and (4) the relatively turbid water of the lagoons and estuaries decrease the foraging efficiency of predators (Blaber & Blaber 1980, Robertson & Blaber 1992). Recently, Laegdsgaard & Johnson (2001) showed by experiment that a combination of these factors determines habitat selection by juvenile fish in mangroves and the authors concluded that the most important aspect of this habitat is the complex structure that provides maximum food availability and minimises predation incidence.

Mangroves and seagrass beds harbour high densities of juvenile reef fish, but the extent to which fishery yields from coral reefs are a function of the presence of these habitats remains unclear (Roberts 1996, Baran 1999, Blaber 2000). This question is related to the concept of 'estuarine-dependence' (Lenanton & Potter 1987, Whitfield 1994, Blaber 2000), in which estuarine-dependent species are defined as those for which estuaries, or similar habitats, are the principal environment for at least part of the life cycle and without which a viable population would cease to exist (Blaber et al. 1989). Since mangroves are the principal habitat in most tropical estuaries, this concept is often linked to dependence on mangroves (Blaber 2000).

The concept of estuarine-dependence is difficult to test by experiment and has so far been tested by comparing presence/absence of juvenile and adult fishes in estuaries versus offshore habitats (e.g. Blaber & Blaber 1980, Lenanton 1982, Blaber et al. 1989). In these studies, fish species which spent the entire post-larval life-cycle in estuaries, and species which were found offshore as adults and occurred as juveniles only in estuaries, were defined as estuarine-dependent. Two problems with these studies are (1) that they all utilised different survey techniques in the different habitats studied, and (2) that it is difficult to understand whether the concept of estuarine-dependence is related to a dependence on estuarine habitats (e.g. mangroves) or on estuarine physico-chemical conditions. To investigate whether fishes also show a dependence on mangrove habitats without the presence of estuarine conditions, and following the comparative approach of above-mentioned studies, we compared densities of juvenile as well as adult reef-associated fishes between offshore habitats (i.e. coral reefs) and truly marine embayments (i.e. disregarding the estuarine component). We improved the study by utilising a single census method in all habitats and by incorporating all major shallow-water habitats, other than mangroves/seagrass beds, which could be used as alternative habitats by juvenile reef fishes. We hypothesised that, as is the case in estuaries, juvenile fish densities are higher in non-estuarine mangroves than in less structurally complex or bare habitats (e.g. Robertson & Duke 1987, Thayer et al. 1987, Laegdsgaard & Johnson 1995). Furthermore, assuming that a strict spatial separation in habitat of juvenile and adult fishes implies an ontogenetic shift between habitats, we investigated the extent to which a coral reef fish population reflects these shifts.

MATERIALS AND METHODS

Study area. The study was carried out in Spanish Water Bay and on the adjacent coral reef in Curaçao, Netherlands Antilles (Fig. 1). The mouth of this sheltered bay is situated on the leeward coast of the island. The bay is connected to the sea by a relatively long and deep channel, which continues into the central part of the bay. Apart from the channel, the bay is relatively shallow, with depths of <6 m. The average daily tidal range is 30 cm (de Haan & Zaneveld 1959). Mean (±SD) water temperature and salinity during the study period (November 1997 to August 1998) for the 12 study sites in the bay were 28.3 ± 0.2°C and 35.4 ± 0.2, respectively. The corresponding values on the reef just outside the bay were 27.5 ± 1.2°C and 35.0 ± 0.2, respectively. The bay has relatively clear water with an average horizontal Secchi disk visibility of 6.2 ± 2.1 m. Mean visibility measured in the same way on the reef just outside the bay was 17.5 ± 4.6 m.

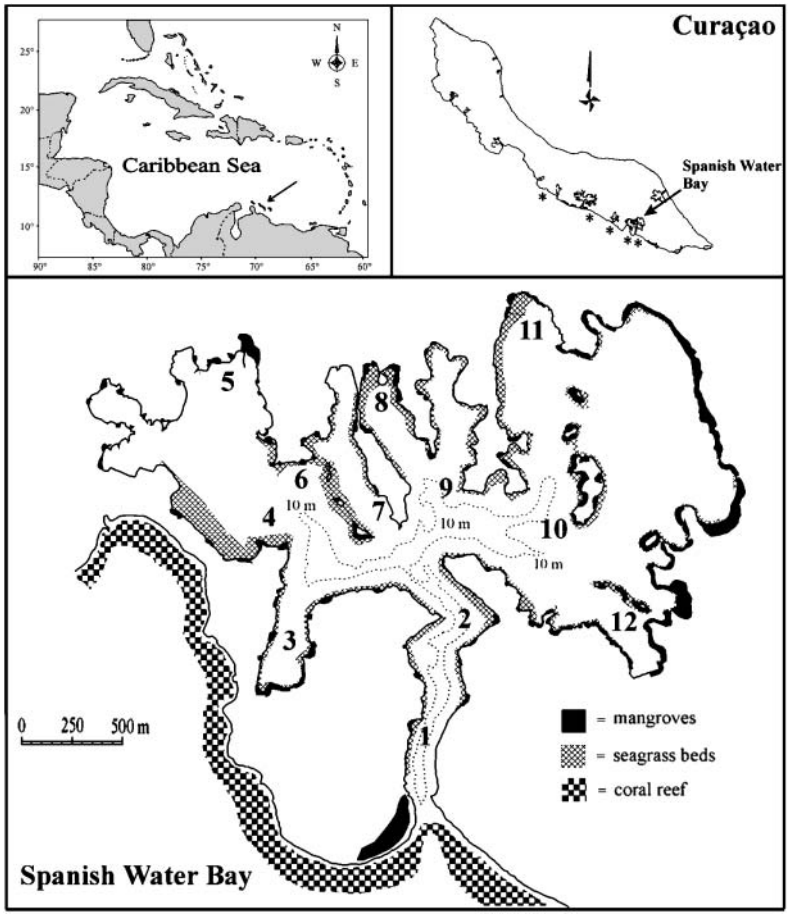

Fig. 1. Map of Spanish Water Bay showing location of study sites in the bay (1 to 12) and on the reef (* in upper right-hand panel). The mud flats generally cover the area between the seagrass beds and the 10 m isobath

Four main habitats of Spanish Water Bay were examined: mangroves, seagrass beds, subtidal mud flats, and the channel. On the adjacent coral reef, 4 depth zones of 2, 5, 10 and 15 m were investigated (Fig. 1). All bay habitats had a muddy substratum.

Red mangrove *Rhizophora mangle* is found along a large part of the shoreline of the bay. The mangrove stands studied were on average 27 ± 11 m long (i.e. distance along the shore) and 1.4 ± 0.5 m wide (i.e. from the outer mangrove fringe to the shoreline), and the average water depth under the mangroves was 0.8 ± 0.2 m.

The shoreline areas of the shallow parts of the bay are dominated by turtle grass *Thalassia testudinum*. This seagrass is found at depths of 40 cm to 3 m, but in the turbid areas of the bay it extends only to a depth of about 1.5 m. Mean seagrass cover was 81 ± 12%. The height of the seagrass was 22 ± 8 cm, at a density of 143 ± 66 shoots m^{-2}.

At depths of 2 to 6 m, where light levels are lower, *Thalassia testudinum* is almost completely replaced by subtidal mud flats with some growth of macroalgal species such as *Halimeda opuntia*, *H. incrassata*, *Cladophora* sp. and *Caulerpa verticillata* (Kuenen & Debrot 1995). The density, areal cover and height of the algal canopy are very low (cover mostly <20%; height <10 cm), and the algae do not provide much shelter for fish.

A channel (11 to 18 m deep) runs from the mouth of the bay to its central parts. The slopes of the channel are covered with fossil reef rocks (10 to 100 cm in length), which are almost completely overgrown by filamentous algae. The soft bottom of the channel is almost completely devoid of vegetation. The fossil reef rocks contain relatively few crevices.

The fringing coral reef extends along the entire SW coast of the island. From the shore, a submarine terrace gradually slopes to a 'drop-off' at depths of approximately 7 to 11 m. At the drop-off, the reef slopes off steeply, sometimes interrupted by a small terrace at depths of 50 to 60 m, ending in a sandy plain at depths of 80 to 90 m. For a detailed description of the reefs of Curaçao see Bak (1975).

Study design. The fish community structure of the 8 selected habitats was determined using a variant of the underwater visual census (UVC) technique first used by Brock (1954). UVC has been used extensively in many studies assessing reef fish communities and has several advantages: it is rapid, non-destructive, inexpensive, it can be used for all selected habitats, the same areas can be resurveyed over time, and the results can be compared with those of many other studies (English et al. 1994). However, UVC also has several disadvantages. Fish behaviour (Brock 1982), census method (Thresher & Gunn 1986), census duration (St. John et al. 1990), census speed (Lincoln Smith 1988), transect width (Cheal & Thompson 1997), degree of replication (Samoilys & Carlos 2000) and observer training (Thompson & Mapstone 1997) are important factors determining UVC accuracy and precision. Densities of fishes and especially of cryptic species are often underestimated (Brock 1982, Sale & Sharp 1983, Willis 2001). A high census speed causes underestimation, but a slow census speed increases

the chance of counting fish entering the transect (Lincoln Smith 1988). An increasing number of replicates improves the precision of density estimation, and smaller transects can be searched more thoroughly but may be too small to assess densities of more mobile fish species (Samoilys & Carlos 2000). Estimation of fish abundance and size clearly differs among observers (St. John et al. 1990, Thompson & Mapstone 1997). Nevertheless it is the most practical and accepted non-destructive method for estimation of reef fish abundance (Thresher & Gunn 1986, Cheal & Thompson 1997).

To decrease the bias of the UVC several efforts were made. Species identification, size estimation and quantification of fish abundance were first thoroughly practised by 3 observers together, which also served to reduce interobserver differences. Size-estimation was practised underwater with objects of known size and this was repeated several times throughout the study. Duration of surveys was between 10 and 15 min in all habitats. Because most of the fishes in the bay habitats remained more or less in the same area, the observer effect on the fish abundance estimates is expected to have been relatively small. Estimation of abundance of Haemulidae and Lutjanidae in the mangroves presented some difficulty because the fish tended to move in-between the prop roots. However, after extensive practise, and with aid of a flashlight in dark parts of the mangroves, the censuses could be done with reasonable accuracy. Densities of *Sparisoma chrysopterum* and *S. rubripinne* (not abundant in the bay) may have been underestimated in the bay habitats since they were easily scared off. At the boulders, some nocturnally active fish species hiding in the crevices may have been underestimated. On the coral reef the high motility of some species of Scaridae may also have affected the fish counts. To account for differences in motility of fishes on the reef, transects were surveyed in 2 runs. On the first run all motile fishes were censused (e.g. Acanthuridae, Lutjanidae, Scaridae) while on the second run less motile and territorial fishes were counted (especially Pomacentridae). Small and cryptic fish species (gobies, blennies, cardinalfishes) were excluded from the census in all habitats.

Twelve study sites in the Spanish Water Bay (Fig. 1), and 5 reef sites on a 12 km long coral reef tract beyond the bay were selected. For each bay habitat, 4 replicate transects were randomly selected at each of the study sites. All transects in all habitats were surveyed during the daytime: once in the period November 1997 to March 1998, and once in August 1998, to increase the sample size. Seasonal variation in density of abundant fishes in the bay was small, compared to the daily variation and the variation in densities between different sites. Large fluctuations in densities of fishes in the bay did not occur, since settlement of juveniles in the bay was either continuous, occurred in many but small numbers of recruits, or was absent. Cocheret de la Morinière et al. (unpubl.) have shown that patterns in habitat utilisation in Spanish Water Bay did not differ for 9 abundant species in 2 consecutive years of sampling, suggesting a stable species-specific pattern in habitat utilisation. The results of night-time surveys in these habitats are reported in Nagelkerken et al. (2000a).

The transects on the seagrass beds, subtidal mud flats and coral reef measured 3×50 m, while those in the channel measured 3×25 m, because of the smaller area of this habitat. Isolated stands of mangrove were selected and surveyed completely. The band of mangroves fringing the shoreline was narrow (up to 2 m), permitting a complete and accurate census. Because the subtidal mud flats were distributed over a relatively large depth range, for a representative sample of the fish community, the mud flat transects were surveyed close to shore at 2 m depth as well as in the deeper parts of the bay at 5 m depth. Snorkelling gear was used for the surveys in the mangroves, seagrass beds and subtidal mud flats at 2 m depth, whereas SCUBA gear was used on the subtidal mud flats at 5 m depth, in the channel and on the coral reef.

The transects were marked by a thin rope, placed at least 30 min before the survey began, in order to minimise disturbance effects. During each survey, individuals of all fish species were counted and size was in first instance estimated in size classes of 2.5 cm. Post-larval stages (i.e. smaller than about 1.0 to 1.5 cm) were excluded because of their small size and their high mortality just after settlement. Pelagic species forming large schools (silversides, scads, herrings, anchovies) were not included in the survey.

For the data analysis a distinction had to be made between juvenile and adult fish densities. Because maturation sizes were only known for 47 of the 114 species, a subdivision based on maximum size was used. Each fish counted was ascribed to 1 of 3 different size classes: small size class ($<^1/_3$ of the species' maximum length), medium size class ($^1/_3$ to $^2/_3$ of the species' maximum length), and large size class ($>^2/_3$ of the species' maximum length). The maximum length for each species was based on data from FishBase (Froese & Pauly 2001; available at: www.fishbase.org). In the fish species for which maturation sizes were available (n = 47) 2 size classes were additionally distinguished: smaller than their maturation size (i.e. juveniles) and larger than their maturation size (i.e. adults). Maturation size as recorded by FishBase is based on minimum maturation size of fish species, and is defined as the size at which fish species acquire first sexual maturity. For the 47 species, density of fishes of the small size

class of fishes was compared to that of juvenile fishes to test the usefulness of the division based on maximum length. These densities appeared to be similar, so the data were extrapolated to the remaining species (n = 67), which means that all fishes of the small size class were considered to be 'juveniles'.

Nagelkerken et al. (2000b) studied the fish community structure in Spanish Water Bay and on the adjacent reef by visual census and distinguished 3 fish species groups (see Table 1): (1) 'nursery species': reef fishes of which the juveniles mainly occur in bays and the adults mainly on the coral reef (i.e. temporary bay residents); (2) 'bay species': fish species of which both juveniles and adults mainly occur in bays and which are not present or occur in low density on the coral reef (i.e. permanent bay residents); and (3) 'reef species': the remaining reef fishes of which all benthic life stages are generally found on the coral reef (i.e. permanent reef residents), but which occasionally visit the bay. In the present study, fish density data of the 3 different fish species groups were compared between the various habitats.

Fish data were analysed for the complete fish community recorded (i.e. 114 species); the analysis in Table 1 is based on the 50 most common species, and Fig. 2 is based on the 47 species for which maturation data were available.

Statistical analysis. For the 47 species for which maturation data were available, a *t*-test was used to test the statistical difference between the density of juveniles and the density of the small size class of the fishes. This was done for the total density of all 47 species pooled, as well as for each species separately, in each of the 8 habitats. For the complete fish community, comparison of total fish density and species richness between habitats was done for each of the 3 size classes using a 1-way ANOVA on log or square-root transformed data, followed by a Tukey HSD multiple comparison test (Sokal & Rohlf 1995). Comparison of total fish density and species richness between different size classes within the same habitat was done with a *t*-test.

Ordination of the complete data set of mean species densities was done on the level of species and families, using the ordination programme Canoco 4.0 (ter Braak & Smilauer 1998). First, a Detrended Correspondence Analysis (DCA) was run to measure the gradient length which indicates how unimodal the species responses are along an ordination axis (ter Braak & Smilauer 1998). It is the range of the sample scores divided by the average within-species SD along the axis, and is expressed in SD units of species turnover. Since the gradient length was short (<4 SD), a Principal Component Analysis (PCA) was done on log-transformed data to compare the fish communities of the various habitats. Scaling was focussed on inter-species correlations, species scores were divided by the SD, and the data were centred by species.

Cluster analysis of mean juvenile fish species densities in the 8 habitats was done using the complete linkage rule and by computing Euclidean distances.

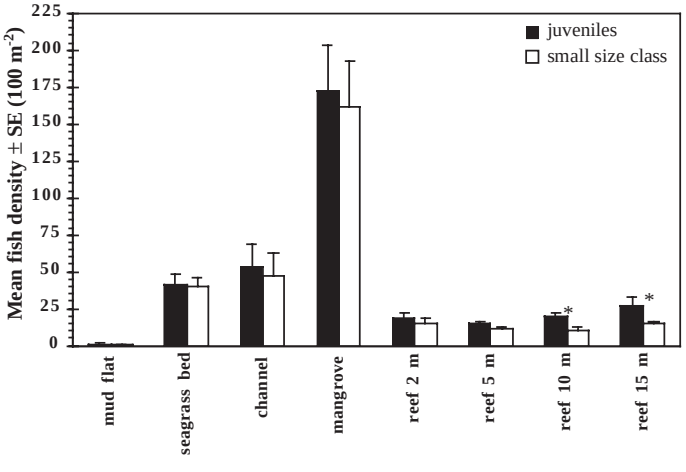

Fig. 2. Mean total density of juveniles (< minimum maturation size) and the small size class of fishes (<$^1/_3$ of species' maximum length) in the 8 selected habitats, for the 47 species for which maturation data were available. *Significant difference ($p < 0.05$)

RESULTS

Total density of juveniles (i.e. fish < maturation size) of the 47 fish species for which maturation data were available did not differ significantly ($p > 0.174$, *t*-test) from that of the small size class (i.e. fish < 1/3 of the species' maximum length) of these species in any of 6 habitats, excluding the reef at 10 m and 15 m depth ($p < 0.048$) (Fig. 2). At species level, the density of juvenile fish versus small size class of fish did not differ significantly ($p > 0.05$) for nearly all of the species either. There were 3 exceptions: *Chaetodon capistratus* had significantly higher ($p < 0.030$, *t*-test) juvenile than small-size-class densities in the seagrass beds, channel, and reef at 5 m and 10 m depth. *Scarus taeniopterus* had higher ($p < 0.001$) juvenile than small-size-class density on the reef at 10 m depth. *Pomacanthus paru* had higher ($p < 0.030$) juvenile than small-size-class density on the reef at 15 m depth. Since the density of juvenile fish of 47 different species (most of which are common species) is largely the same as that of the small size class of the same fish species, we extrapolate the results to the complete fish fauna (N = 114) and from here on we call the small size class of fish 'juveniles', the medium size class of fish 'small adults', and the large size class of fish 'large adults'.

Total density of juveniles for the complete fish community was highest on the coral reef and in the mangroves (Fig. 3a). Densities in other bay habitats were significantly lower than in the mangroves, and extremely low on the subtidal mud flats. Compared to the juveniles, small adults showed significantly lower densities in various shallow-water habitats, viz. seagrass beds, mangroves and the reef at 2 m depth ($p < 0.020$, *t*-test), as opposed to a (non-significantly) higher density at 10 m depth (Fig. 3a). Large adults were almost completely restricted to the deeper reef (i.e. 5 to 15 m depth).

Mean species richness of the complete fish community showed a similar pattern to that of mean fish density (Fig. 3b). Two main differences were that firstly, species richness of juveniles in the mangroves was more similar to that of other bay habitats than to that of the reef habitats and secondly, species richness at the deeper reef (5, 10, 15 m depth) was significantly higher in the small adults than in the juveniles ($p < 0.001$, *t*-test).

The 3 distinguished species groups showed marked differences in fish densities between habitats. Juveniles of the nursery species group showed highest fish densities in the mangroves, followed by the seagrass beds and channel (Fig. 4a). On the subtidal mud flat and on the reef their densities were very low. Compared to the juveniles, the small adults showed significantly lower densities ($p < 0.049$, *t*-test) at the subtidal mud flats, seagrass beds and mangroves, as opposed to significantly higher densities ($p < 0.027$) on the deep reef (10 m and 15 m depth). The large adults were absent from the bay and most abundant on the deep reef at 15 m depth.

Juveniles of the reef species group showed similar densities on the 4 depth zones (Fig. 4b). Compared to the juveniles, the small adults showed a significantly lower density ($p < 0.019$, *t*-test) at the reef of 2 m depth. The large adults were almost completely absent from the bay habitats.

Juveniles, small adults as well as large adults of the bay species group showed highest densities in the mangroves, and were almost absent on the coral reef at 5 to 15 m depth (Fig. 4c).

Principal Components Analysis (PCA) of juvenile fish densities of the complete fish community showed a clear separation be-

Table 1. Mean densities (ind. per 100 m^2) of juveniles, small adults and large adults of the 50 most common fish species (density > 0.5 ind. per 100 m^2) in the various bay and reef habitats. Fishes are categorised into 4 groups and several subgroups by species showing comparable ontogenetic shifts in habitat utilisation from juvenile to adult habitat. Outlined gray areas indicate most important habitat; ordinary gray areas indicate other important habitats (i.e. density > 50% of density in most important habitat). M = mangrove, S = seagrass bed, C = channel, MF = mud flat. 2 m, 5 m, 10 m and 15 m = depth zones on the coral reef. N = nursery species group, R = reef species group, B = bay species group (see text for definition). OT = outside transects. *Defined as a bay species because densities in rocky bay habitats (notches, boulders) were much higher than on the reef (Nagelkerken et al. 2000b)

	Species group	Juveniles								Small adults								Large adults							
		M	S	C	MF	2 m	5 m	10 m	15 m	M	S	C	MF	2 m	5 m	10 m	15 m	M	S	C	MF	2 m	5 m	10 m	15 m
1a) Mangrove ⇒ Reef																									
Chaetodon capistratus, foureye butterflyfish	N	4.0	0.4	1.6	0.0	–	–	–	–	5.1	0.6	5.5	0.0	2.0	3.2	2.9	2.1	–	–	–	–	0.0	–	–	0.1
Haemulon flavolineatum, french grunt	N	62.3	16.9	0.8	0.1	–	0.9	–	–	20.4	0.8	3.6	0.0	0.5	3.1	2.7	2.2	–	–	–	–	–	–	OT	–
Haemulon parra, sailors choice	N	6.0	0.0	–	–	–	–	–	–	0.1	0.0	–	–	–	–	–	–	–	–	–	–	–	–	–	OT
Haemulon sciurus, bluestriped grunt	N	20.5	2.4	–	0.0	–	–	0.1	–	1.4	0.0	0.1	–	0.0	0.2	0.4	0.1	–	–	–	–	–	–	OT	–
Lutjanus apodus, schoolmaster	N	27.4	0.2	0.3	0.0	0.0	0.3	0.2	0.1	0.1	–	–	–	–	0.0	0.2	0.1	–	–	–	–	–	–	–	0.1
Lutjanus mahogoni, mahogany snapper	N	1.2	0.0	0.0	–	–	–	0.0	–	–	0.0	0.0	–	–	0.1	0.3	0.1	–	–	–	–	–	–	–	–
Scarus guacamaia, rainbow parrotfish	N	0.7	0.0	–	0.0	–	–	–	–	–	–	–	–	–	–	0.0	–	–	–	–	–	–	–	–	–
Sparisoma chrysopterum, redtail parrotfish	N	1.3	0.3	0.3	–	0.5	0.1	0.0	0.0	–	0.0	2.4	–	0.7	0.3	0.1	0.1	–	–	–	–	OT	OT	–	–
Sphyraena barracuda, great barracuda	N	1.3	0.1	–	0.0	–	0.0	0.0	0.0	–	–	–	–	–	OT	OT	OT	–	–	–	–	–	–	–	–
1b) Channel ⇒ Reef																									
Acanthurus chirurgus, doctorfish	N	0.7	0.6	1.2	–	0.0	–	–	–	0.4	0.1	2.5	0.1	–	0.2	0.8	0.2	–	–	–	–	–	OT	–	–
Haemulon chrysargyreum, smallmouth grunt	R	0.1	–	0.2	–	–	–	–	–	0.1	0.2	0.1	–	–	0.1	1.1	5.6	–	–	–	–	–	0.3	0.1	0.4
Holocentrus adscensionis, squirrelfish	R	–	–	1.3	–	0.0	0.0	–	0.0	–	–	0.4	–	–	–	–	–	–	–	–	–	–	–	–	OT
Scarus coeruleus, blue parrotfish	N	–	0.4	0.9	0.0	0.2	0.0	–	–	–	–	–	–	–	–	OT	OT	–	–	–	–	–	–	–	–
Scarus iserti, striped parrotfish	N	7.3	15.2	29.6	0.1	3.9	3.1	3.2	1.1	–	0.0	1.3	0.0	2.7	1.5	1.7	1.1	–	–	–	–	0.0	0.0	–	–

1c) Mangrove/Channel ⇒ Reef																									
Lutjanus griseus, gray snapper	N	4.5	0.4	5.2	0.3	–	–	0.0	–	0.1	0.0	–	0.0	–	–	–	–	–	–	–	–	–	–	–	OT
Ocyurus chrysurus, yellowtail snapper	N	4.6	1.9	3.5	0.2	0.0	0.5	0.8	0.5	–	–	–	–	–	–	–	0.0	–	–	–	–	–	–	–	–
1d) Shallow reef ⇒ Deeper reefs																									
Abudefduf saxatilis, sergeant major	R	–	–	–	–	0.3	–	–	–	–	–	–	–	0.0	–	0.5	0.5	–	–	–	–	–	–	–	0.1
Halichoeres radiatus, puddingwife	R	–	–	–	–	2.5	1.2	0.2	0.1	–	–	–	–	–	–	0.0	–	–	–	–	–	–	–	–	–
2) Shallow reef ⇒ Reef																									
Halichoeres maculipinna, clown wrasse	R	–	0.0	0.3	–	14.0	3.3	0.4	–	–	0.2	0.9	–	14.6	6.0	2.2	0.4	–	–	–	–	0.2	0.1	0.2	–
Stegastes diencaeus, longfin damselfish	R	–	–	–	–	14.0	5.0	0.1	0.2	–	–	–	–	13.0	12.9	13.3	1.7	–	–	–	–	0.9	0.1	0.2	–
Thalassoma bifasciatum, bluehead wrasse	R	–	0.1	0.5	–	141.6	80.4	59.9	20.9	0.3	0.0	0.3	–	5.5	6.1	4.0	0.8	–	–	–	–	–	–	–	–
3a) Within bay habitats																									
Archosargus rhomboidalis , sea bream	B	2.0	0.3	–	–	–	–	–	–	2.7	0.3	–	0.4	–	–	–	–	–	–	–	–	–	–	–	–
Eucinostomus sp. 1, mojarra sp. 1	B	0.6	0.7	–	0.0	–	–	–	–	0.2	0.0	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Eucinostomus sp. 2, mojarra sp. 2	B	0.2	1.7	–	0.1	–	–	–	–	0.2	0.6	–	0.0	–	–	–	–	–	–	–	–	0.0	–	–	–
Gerres cinereus, yellowfin mojarra	B/N	16.9	0.1	–	0.0	–	–	–	–	0.3	0.1	0.1	0.0	0.1	0.1	–	–	–	–	–	–	–	–	–	–
Stegastes leucostictus, beaugregory	B	–	–	0.0	–	–	–	–	–	0.3	0.1	1.6	–	–	–	–	–	3.3	0.2	1.0	0.0	–	–	–	–
3b) Shallow reef ⇒ Shallow reef																									
Acanthurus bahianus, ocean surgeon	R	–	0.0	0.0	–	4.4	0.6	0.0	0.2	–	0.0	–	–	11.7	5.0	3.8	1.1	–	–	–	–	–	–	–	–
Acanthurus coeruleus, blue tang	R	0.0	–	0.1	–	0.5	0.1	0.1	0.1	–	–	–	–	5.5	0.8	1.6	0.8	–	–	–	–	–	–	–	–
Halichoeres bivittatus, slippery dick	R	–	0.6	2.0	–	22.6	16.3	0.2	0.1	0.1	0.4	1.8	–	5.9	2.7	–	–	–	0.0	0.1	–	–	–	–	–
Microspathodon chrysurus, yellowtail damselfish	R	–	–	–	–	3.0	2.8	1.0	0.4	–	–	–	–	3.6	2.2	1.7	0.2	–	–	–	–	3.2	0.5	0.2	–
Scarus vetula, queen parrotfish	R	–	–	–	–	1.0	0.4	0.1	0.1	–	–	–	–	1.7	0.7	1.0	0.3	–	–	–	–	–	–	–	–
Sparisoma rubripinne, redfin parrotfish	R	–	–	–	–	0.1	0.0	–	–	–	–	–	–	1.2	0.2	0.0	–	–	–	–	–	–	0.0	–	–
Stegastes dorsopunicans , dusky damselfish•	B	0.0	–	–	–	5.5	–	–	–	0.4	–	0.3	–	2.9	–	–	–	0.1	–	–	–	–	–	–	–
3c) Deep reef ⇒ Deep reef																									
Canthigaster rostrata, sharpnose puffer	R	–	–	0.1	–	0.0	0.3	2.3	4.3	–	–	0.5	–	–	0.2	0.6	1.2	–	–	–	–	–	–	–	–
Cephalopholis cruentatus, graysby	R	–	–	–	–	–	0.0	0.2	0.3	–	–	0.0	–	0.0	0.1	0.7	1.0	–	–	–	–	–	–	0.0	0.0
Chromis cyanea, blue chromis	R	–	–	–	–	–	0.5	41.6	32.2	–	–	–	–	0.1	4.3	34.9	33.1	–	–	–	–	–	–	–	–
Chromis multilineata, brown chromis	R	–	–	–	–	0.8	7.3	13.5	0.3	–	–	0.5	–	2.8	6.1	34.7	11.0	–	–	–	–	–	–	0.3	2.7
Clepticus parrae, creole wrasse	R	–	–	–		0.2	–	1.3	8.6	–	–	–	–	0.4	0.1	2.6	2.2	–	–	–		–	–	0.0	–
Gramma loreto, royal gramma	R	–	–	–	–	–	–	–	2.2	–	–	–	–	–	–	0.8	4.3	–	–	–	–	–	–	–	0.2
Halichoeres garnoti, yellowhead wrasse	R	–	–	–	–	1.0	9.9	19.7	19.4	–	–	–	–	0.8	6.7	8.2	9.0	–	–	–	–	–	0.1	–	–
Halichoeres pictus, rainbow wrasse	R	–	–	–		–	–	–	0.4	–	–	–	–	0.3	7.4	12.5	0.9	–	–	–		0.1	0.4	1.4	–
Scarus taeniopterus, princess parrotfish	R	–	–	–	–	1.1	0.6	1.3	5.5	–	–	–	–	1.5	1.1	3.6	3.6	–	–	–	–	–	–	0.0	0.0
3d) Reef ⇒ Reef																									
Serranus tigrinus, harlequin bass	R	–	–	–	–	0.4	2.0	1.9	2.5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Sparisoma aurofrenatum, redband parrotfish	R	–	0.0	0.2	–	0.9	2.8	2.3	2.3	–	0.0	0.6	–	1.5	2.0	2.4	2.2	–	–	0.0	–	0.2	0.2	0.9	0.6
Stegastes partitus, bicolor damsel	R	–	–	1.0	–	23.0	41.5	69.2	60.6	–	–	7.0	–	14.0	79.1	121.0	85.0	–	–	0.5	–	2.3	33.3	39.4	65.3
Stegastes planifrons, threespot damselfish	R	–	–	1.2	–	0.8	4.7	6.4	8.7	0.1	0.0	2.8	–	0.2	7.5	19.6	20.1	–	–	–	–	–	0.1	0.8	–
4) Miscellaneous habitats																									
Hypoplectrus unicolor, butter hamlet	R	0.1	0.0	0.2	–	–	–	0.2	0.0	0.5	0.1	1.9	–	0.0	0.1	0.2	0.1	–	–	0.1	–	0.0	–	0.0	0.1
Mulloidichthys martinicus, yellow goatfish	R	0.8	0.0	–	–	0.4	–	0.7	1.4	0.4	0.0	0.1	0.4	0.1	0.3	5.9	5.4	–	–	0.0	–	–	–	–	–
Sparisoma viride, stoplight parrotfish	R	0.7	0.0	1.5	–	1.4	1.3	1.3	0.9	–	–	1.0	–	1.3	1.0	1.3	1.0	–	–	–	–	–	–	–	–
No juveniles encountered																									
Myripristis jacobus, blackbar soldierfish	R	–	–	–	–	–	–	–	–	–	–	–	–	0.3	1.5	8.5	9.1	–	–	–	–	–	–	0.0	–

tween the reef species group on the coral reef and the nursery and bay species group in the bay (Fig. 5a). The bay habitats showed a higher similarity in species composition of juveniles than the reef habitats (Figs. 5a & 6) where many species were either observed at 2 and 5 m depth or at 10 and 15 m depth. Compared to the PCA of juvenile fish, PCA of small adults showed a lower number of nursery species in the bay but a higher number of nursery species on the reef (Fig. 5b). PCA of the large adults showed complete absence of nursery species in the bay (Fig. 5c).

The 50 most common fish species could be divided into 4 different 'ontogenetic' groups, based on densities of juveniles and adults in the selected habitats (Table 1). The first group consisted of 18 fish species of which the juveniles were almost exclusively found in shallow-water habitats (i.e. mangrove, channel, or shallow reef of 2 m depth), and the adults were most abundant on the (deeper) reef. This group was almost completely represented by nursery species in the mangroves and channel, and by members of the reef species group on the shallow reef. The second group consisted of 3 reef fish species of which the juveniles were most abundant on the shallow reef of 2 m, and the adults were abundant on all reef zones between 2 and 15 m depth. The third group consisted of 25 fish spe-

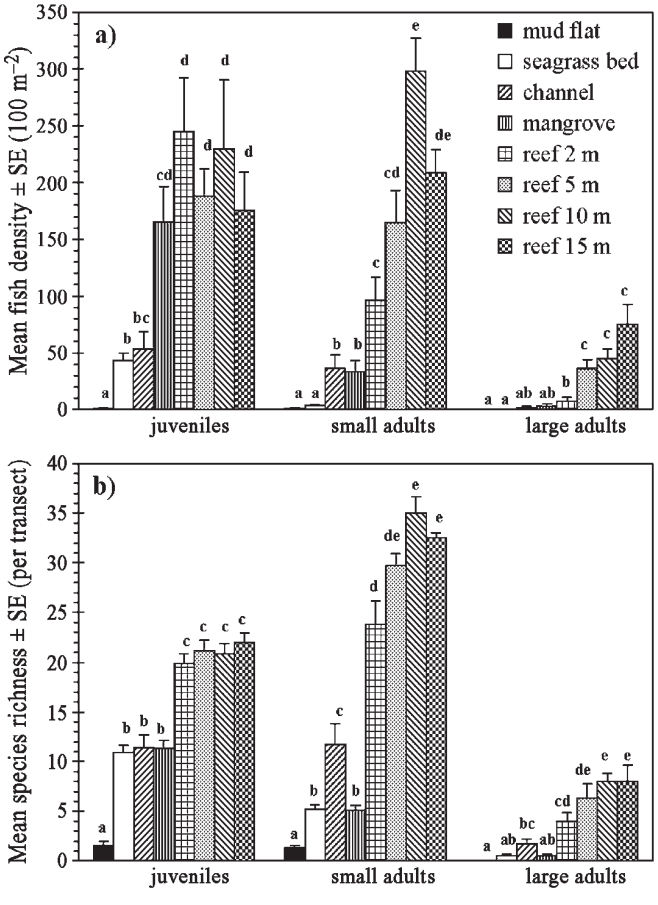

Fig. 3. (a) Mean total fish density and (b) species richness of juveniles, small adults and large adults of the complete fish community at the 8 selected habitats. Different letters indicate that means differ significantly (Tukey HSD test, $p < 0.05$)

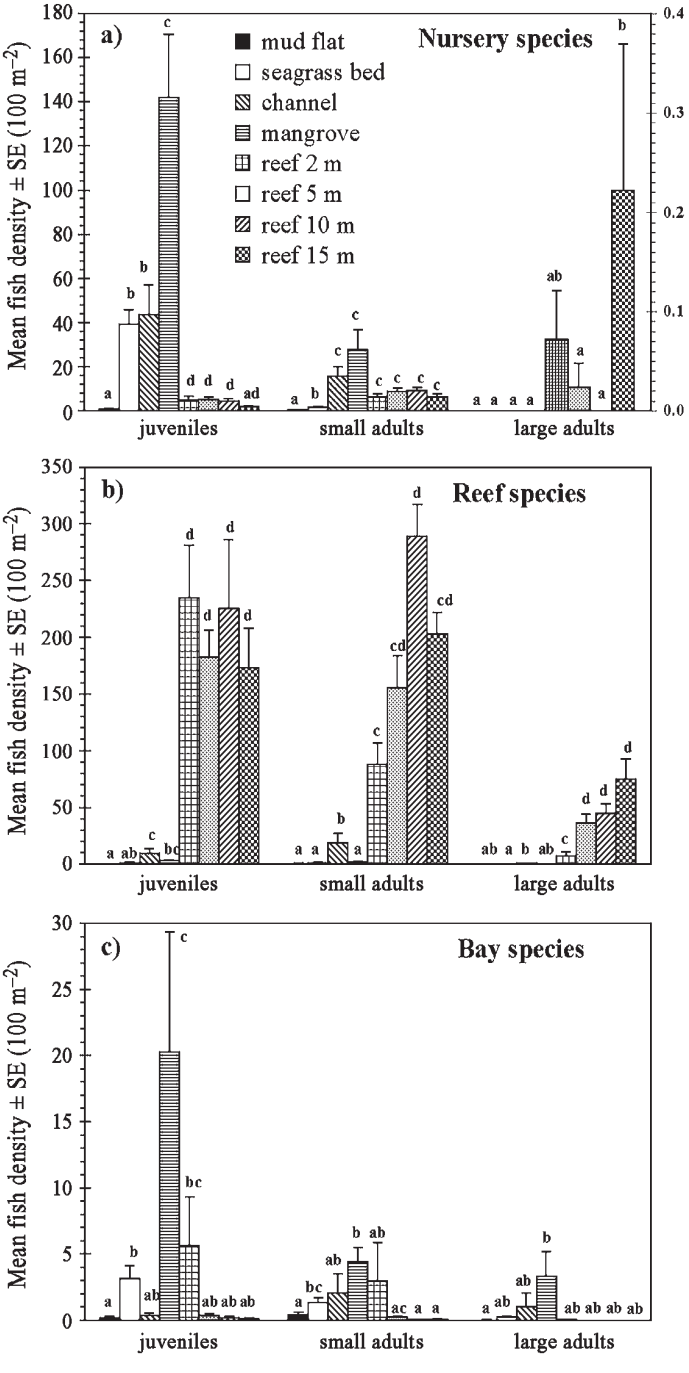

Fig. 4. Mean total fish density of the (a) nursery, (b) reef and (c) bay species groups for juveniles, small adults and large adults at the 8 selected habitats. Right-hand *y*-axis in (a) represents densities of large adults. Different letters indicate that means differ significantly (Tukey HSD test, $p < 0.05$)

cies of which the juveniles and adults were found in more or less the same habitat; for 5 species this was various bay habitats, for 7 species the reef of 2 m depth, for 9 species the reef of 10 to 15 m depth, and for 4 species the entire reef. This group was represented by bay species in the bay habitats and by reef species in the reef habitats. The 4th group consisted of 3 fish species of which the juveniles and adults were both found in a wide range of bay and reef habitats and no clear pattern could be detected. This small group was represented by members of the reef species group. For 1 species no juveniles were found. Of the 50 species, 11 species showed much higher densities in mangroves than in other habitats.

PCA of total fish densities (i.e. complete fish community) within families showed a clear separation between bay and reef habitats (Fig. 7a). The bay habitats, especially the mangroves, were dominated in terms of density by abundant fish families such as Haemulidae, Lutjanidae and Gerreidae, while the abundant Scaridae were found in about equal densities in bay and reef habitats. All other abundant fish families reached highest densities on the different reef depth zones which showed a high degree of similarity. PCA of total species richness within families showed a similar pattern to that of total fish density (Fig. 7b). All families which were dominant in the bay habitats in terms of density also dominated in the bay in terms of species richness, except Holocentridae. Fish species were more evenly distributed among the bay habitats in terms of species richness than was the case for fish density.

DISCUSSION

The present study shows that the structurally complex coral reef and mangroves harbour a much higher total density of juvenile fish than the less structurally complex channel, seagrass bed and mud flat when considering the complete fish community. The fact that mangroves and coral reef habitats show similar total juvenile fish densities, although they occur in different environments, supports the hypothesis that presence of structure is more important in attracting fish than the characteristics of the habitat (Bell et al. 1987, Jenk-

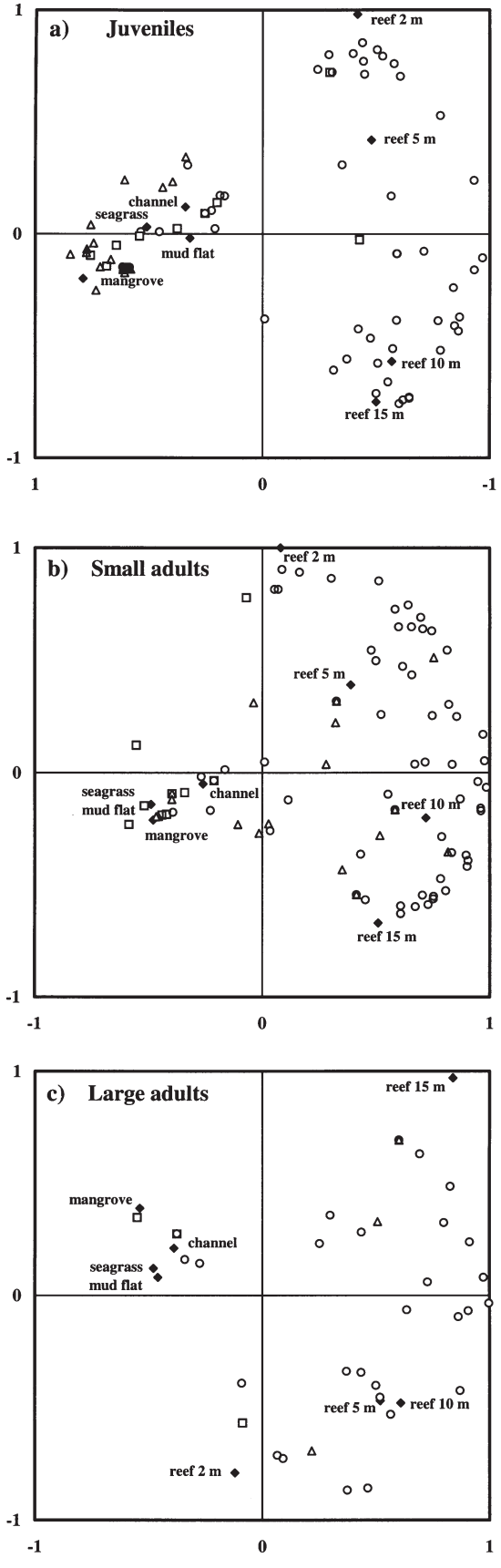

Fig. 5. Principal Components Analysis (PCA) of fish species densities of the complete fish community in the 8 selected habitats for (a) juveniles, (b) small adults and (c) large adults. Eigenvalues of the first and second PCA axis are (a) 0.56 and 0.20, (b) 0.67 and 0.19, and (c) 0.80 and 0.10, respectively. (△) Nursery species group, (○) reef species group, (□) bay species group, (◆) habitat type

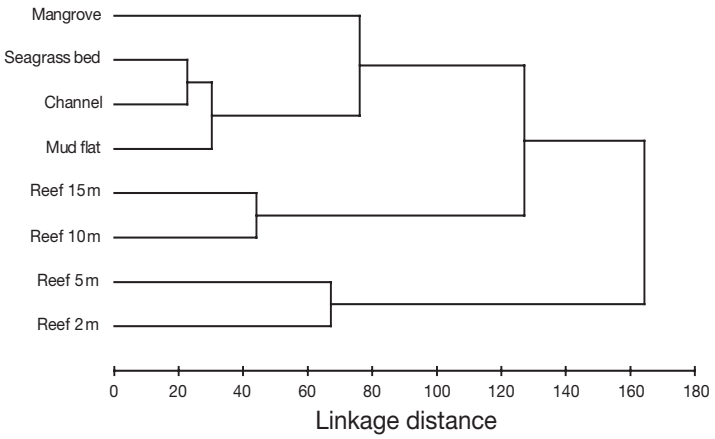

Fig. 6. Cluster analysis of juvenile fish densities of the complete fish community in the 8 selected habitats

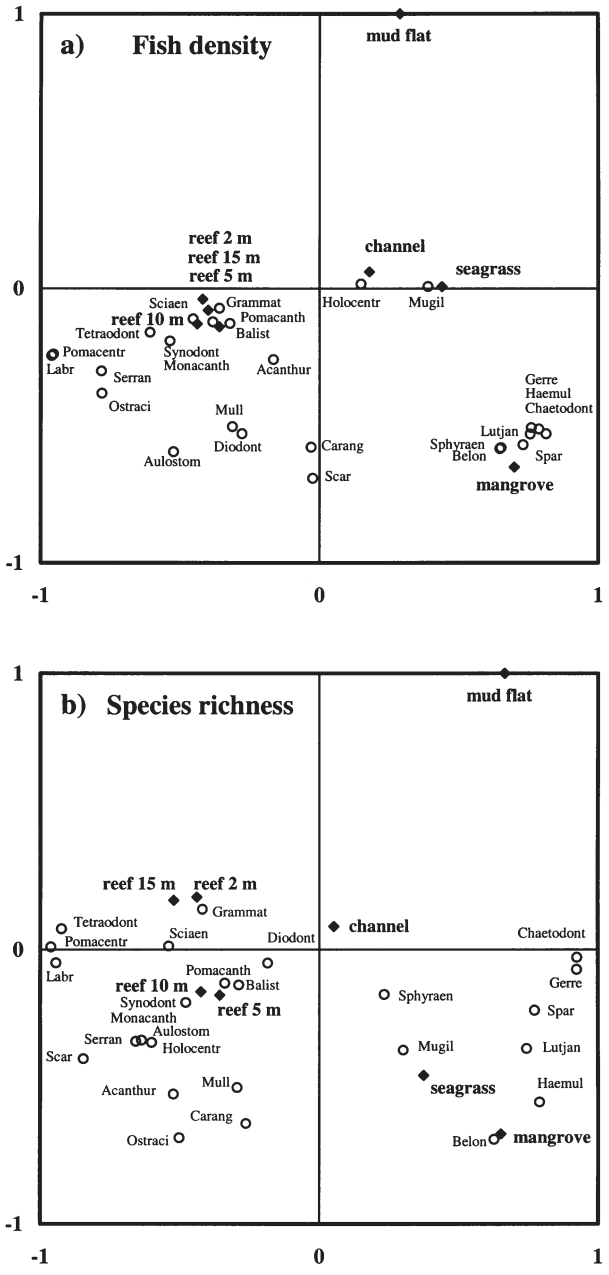

Fig. 7. Principal Component Analysis (PCA) of (a) total species density and (b) total species richness of juvenile fish for different fish families (based on the complete fish community) in the 8 selected habitats. Eigenvalues of the first and second PCA axis are (a) 0.72 and 0.15, and (b) 0.71 and 0.10, respectively. Family names are abbreviated by omitting 'idae' at the end

ins & Wheatley 1998). Several studies have already shown that total fish density is positively related to habitat complexity (Luckhurst & Luckhurst 1978, Grigg 1994, Chabanet et al. 1997) and the same was observed in the present study: juvenile fish densities of the complete community and degree of structural habitat complexity decreased in the following order: coral reef habitats/mangroves, channel/seagrass beds, and subtidal mud flats. Other studies have also found that total fish densities are highest in mangroves, followed by seagrass beds (Robertson & Duke 1987, Thayer et al. 1987, Laegdsgaard & Johnson 1995) and sand flats (Sedberry & Carter 1993, Nagelkerken et al. 2000b).

For both the nursery and bay species group it was only the mangrove habitat that contained a high density of juvenile fish, whereas for the reef species group this was only the case for the coral reef. Hence, our hypothesis that in non-estuarine conditions juvenile fish densities are higher in mangroves than in less structurally complex or bare habitats appears to be true for total juvenile fish density of the nursery and bay species group, and for juvenile density of 11 nursery and bay species specifically (see Table 1). Aside from their high structural complexity, the mangroves may harbour high densities of fish because of the shading effect of the overhanging canopy. Helfman (1981) showed that fish hovering in the shade have 2 advantages over non-shaded fish: they are better in seeing objects approach (e.g. predators) and they are more difficult to be seen. Laegdsgaard & Johnson (2001) further suggested that for most fishes presence of food in the mangroves is a more important selection criterion than their structural complexity. In the present study, however, food probably played an insignificant role. Most fishes in the mangroves were nocturnal zoobenthivores, which utilise the mangroves as shelter sites during daytime; at night, when predation pressure is lower, they migrate to the seagrass beds and subtidal mud flats to feed (Nagelkerken et al. 2000a). This suggests that reduction of predation risk is the primary factor responsible for the high juvenile fish densities in these non-estuarine mangroves during daytime.

Total species richness of juvenile fish showed almost the same pattern as that of total fish density, with the main exception that species richness in the mangroves was relatively low and more similar to that of other bay habitats (i.e. channel and seagrass bed) than to that of the coral reef. Luckhurst & Luckhurst (1978) showed that on the reefs of Curaçao fish species richness was even more highly correlated to structural complexity of habitat than was the case for fish density, and attributed this to the fact that a higher complexity results in a greater diversity of shelter sites for both fish and their prey (i.e. food), and thus enhances species richness. The lower food abundance in mangroves than in other habitats such as seagrass beds (Sheridan 1992, Nagelkerken et al. 2000a) may therefore explain the relatively low species richness of fish in the mangroves, because this makes them a less attractive habitat for diurnally active species.

All nursery and bay species showed highest juvenile densities in the bay habitats, and most of these species showed absence or very low juvenile densities on the coral reef. Other habitats covering large surface areas which could harbour high densities of juvenile fish are not present on the island of Curaçao; hence the juveniles of these species would be considered as dependent on bay habitats when following the approach used in field studies for evaluating the concept of estuarine-dependence (Blaber & Blaber 1980, Lenanton 1982, Blaber et al. 1989). Since no estuarine influence is present in these bay habitats, for these circumstances, we introduce the concept of 'bay habitat dependence' and define bay habitat dependent species as 'species for which bay habitats are the principal environment for at least part of the life cycle and without which a viable population would cease to exist', where bay habitats could be a single or combination of habitats located in shallow-water embayments, bays or lagoons with marine conditions. Although the data suggest that bay habitats are the principal environment for juveniles of most nursery and bay species, it is difficult to prove whether a viable population would cease to exist with absence of these habitats. Shulman & Ogden (1987) observed for *Haemulon flavolineatum* that 95% of recruits settled in a seagrass-dominated lagoon and only 5% directly on the reef, yet they calculated that this 5% was sufficient to sustain the reef population. Care should therefore be taken in correlating high densities of juveniles with a high contribution to population growth. This problem has also not been solved for the concept of estuarine-dependence (Blaber 2000). Gaining conclusive experimental evidence is difficult, but extra support for our concept is provided by 2 comparative studies. Nagelkerken et al. (2001a) compared different bays on Curaçao with and without mangroves/seagrass beds. They found that juveniles of nursery species were almost completely absent from bays without these habitats. Juveniles of some nursery species were highly associated with presence of mangroves and seagrass beds, while others only with seagrass beds. In a second study, Nagelkerken et al. (2002) compared Caribbean islands with bays containing mangroves and seagrass beds with islands completely lacking bays or comparable shallow-water environments with mangroves/seagrass beds. They found that adults of many nursery species were either absent or present in very low density on the coral reef of islands lacking bays with mangroves and seagrass beds.

For several species, juveniles and adults showed a separation in habitat. Since fishes were not tagged the different distribution is only suggestive for an ontogenetic movement between habitats. Other models, such as differential growth and mortality between the different habitats, cannot be excluded (Gillanders 1997). A difference in fishing pressure, where for example adults are heavily fished in the bay, may also be an alternative model, but this was not the case in Spanish Water Bay. If the differential distribution of juveniles in habitats is indicative of ontogenetic habitat shifts, at least 21 common species can be considered to show such a pattern. Such inferred shifts may then occur from mangrove to reef (9 species), from channel to reef (5 species), from mangrove/channel to reef (2 species) and from shallow reef to deep reef (2 species). For 3 species a partial ontogenetic shift (shallow reef to entire reef) may be inferred, where part of the adult population is still common in the juvenile habitat. Lindeman et al. (2000) suggested, on the basis of a qualitative study, ontogenetic habitat shifts for at least 50 Caribbean reef fish species, including all species of Haemulidae and Lutjanidae of the present study, but in addition many species of Serranidae. These species may thus show a long distance post-settlement life-cycle migration, where juveniles grow up in shallow-water habitats and migrate as (sub)adults across the shelf towards the deeper reef. The function of this inferred migration may be to alleviate intra- or interspecific competition (Roberts 1996, Cocheret de la Morinière et al. 2002). Such ontogenetic shifts could explain why, in the bay habitats and shallow reef total density, total species richness and density of nursery species were higher for juveniles than for small adults, and why these factors were higher on the deeper reef for small adults than for juveniles. If bay habitats are the primary habitat for the juveniles of some species, they may contribute to the species richness and fish density on the coral reef when ontogenetic shifts occur. It should be noted that the juvenile fish population censused in the bay habitats consisted primarily of larger juveniles (mean size of nursery species: 5.4 to

18.4 cm, Nagelkerken et al. 2000b), and did not include larval fish or small juveniles (<2.5 cm). Large recruitment pulses occurred outside of the census periods and it is known that in the first few weeks after settlement these small fish generally show very high mortality (Shulman & Ogden 1987). Hence, a possible contribution of the bay habitats to the reef fish population would in fact be larger than would be the case when the high densities of newly settled fishes would have been included in the analysis.

The different habitats studied could also be distinguished on the basis of fish families. Principal components analysis showed that in terms of juvenile density and number of species most families were dominant in 1 or other of the 2 environments, viz. the coral reef or the bay habitats. This pattern suggests a high association for juvenile fish between fish family and habitat, but seems to contradict the strategy of spatial segregation by congeneric species to avoid direct overlap in resource use (Werner & Gilliam 1984). This apparent conflict is non-existent, however, because within the coral reef and bay environments different juvenile size classes of different congeneric species often utilise different habitats (Nagelkerken et al. 2000c, Cocheret de la Morinière et al. 2002). It is difficult to determine why juveniles of some families are more abundant on the coral reef than in the bay habitats and vice versa. For at least some families there appears to be a plausible explanation. Pomacentridae almost exclusively occur on the reef and it has been argued that these largely territorial fish cannot afford to recruit into bay habitats and take the risk that the adult habitat cannot be found (Shulman 1985). Juveniles of Chaetodontidae, Haemulidae and Lutjanidae are all zoobenthivores, and the higher abundance of zoobenthos in the bay habitats may explain their higher densities in these habitats (Nagelkerken et al. 2001b). Mugilidae and Gerreidae are typical bay species which spend their entire life cycle in the bay (Nagelkerken et al. 2000b).

The various habitats of Spanish Water Bay appear to primarily harbour juveniles of fishes which are associated with reefs as adults. This becomes more clear when considering that in terms of fish density the bay habitats are almost entirely dominated by juveniles of these reef-associated species (i.e. nursery species): mangrove 85%, seagrass beds 87%, channel 66%, subtidal mud flat 48%. Since these species are found on the coral reef as adults, only relatively few fish species appear to be present in the bay during their entire benthic life cycle, viz. the less abundant bay species. This is in contrast with estuaries where, aside from marine species, estuarine species and freshwater species can also be found and a much higher density of permanent residents occurs (Robertson & Blaber 1992, Blaber 2000). Considering the high density of juvenile reef-associated fish in Spanish Water Bay, ontogenetic movement to the reef would imply a strong interaction between the bay and reef, which would be an argument for conservation, management and sustainable use of bay habitats. This would contrast the situation in the Pacific, where Birkeland & Amesbury (1988) and Thollot & Kulbicki (1988) found that only few interactions exist between different coastal fish communities and suggested that each habitat may be self-sufficient.

In conclusion, the present study shows that non-estuarine mangroves do harbour much higher densities of juvenile fishes than adjacent seagrass beds, channel and mud flats, but similar juvenile densities as the adjacent coral reef, which is probably related to structural complexity of habitat. For a number of nursery and bay species, juvenile fish were found almost exclusively in the mangroves and sometimes to a lesser extent in other bay habitats, but rarely on the coral reef, giving birth to a concept of 'bay habitat dependence'. The differential densities of juvenile and adults in various habitats is suggestive for partial or complete ontogenetic habitat shifts for at least 21 of the 50 most common reef species.

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